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# Habitat Selection by Elk before and after Wolf Reintroduction in Yellowstone National Park, Wyoming

by

Julie S. Mao

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

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**ABSTRACT**

Prey species select habitat in an attempt to obtain necessary resources (food, mates, shelter, etc.) while also avoiding predation. I examined whether habitat selection by elk (*Cervus elaphus*) changed following the reintroduction of wolves (*Canis lupus*) into Yellowstone National Park in 1995. Using conditional fixed-effects logistic regression to build habitat selection models, I compared seasonal habitat selection by elk before and after wolf reintroduction based on weekly elk radiolocations taken in 1985-1990 (prewolf) and 2000-2002 (postwolf). In summer, when wolf activity was centered around dens and rendezvous sites, elk avoided wolves by selecting higher elevations, less open habitat, more burned forest, and, in high wolf density areas, steep slopes. In winter, elk did not spatially separate themselves from wolves on a weekly timescale and, compared to the prewolf period, they selected for more open habitats after wolf recovery. Elk appear to use habitat selection to avoid wolves in summer, but must rely on behavioral anti-predator strategies such as grouping in winter.

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## INTRODUCTION

Habitat selection is the process by which organisms attempt to maximize fitness through preferential use of habitat types (Fretwell and Lucas 1970, Rosenzweig 1985, Morris 2003). In predator-prey systems, habitat selection by prey may require making a tradeoff between the acquisition of resources (e.g., forage, mates, shelter, etc.) on the one hand, and avoidance of predators on the other hand (Werner and Anholt 1993). To reduce the risk of predation, prey make behavioral decisions to decrease the probabilities of encounter, attack, and capture, and the time spent vulnerable to predation (Lima and Dill 1990). Anti-predator behaviors by prey include distancing themselves from a predator, keeping vigilant to detect predators, and using habitat structure to hide from predators or to evade pursuing predators once attacked (Bergerud et al. 1984, Elgar 1989, Kie 1999). Predator-induced habitat selection can have population level consequences if indeed predator avoidance comes at the cost of foraging or reproduction (Sinclair and Arcese 1995, Sutherland 1996:157-166, Lima 1998). However, habitat selection also can stabilize predator-prey systems by giving prey spatial or temporal refuges from predators (Huffaker et al. 1963, Pimental et al. 1963, Taylor and Pekins 1991). Habitat shifts and predator avoidance by individual prey can buffer demographic declines due to predation, thus facilitating the persistence of the prey population (Lima 1998).

Habitat selection by elk (*Cervus elaphus*) has been well documented in North American populations (reviewed in Slovkin et al. 2002). Elk are habitat generalists, once distributed throughout much of the continent (O'Gara and

Dundas 2002). Elk are primarily grazers, but they also browse in fall and winter; they use forest edges for thermal and hiding cover, and often will use sagebrush habitat for calving; and they select low to mid-slopes, particularly south-facing aspects (Houston 1982, Slovkin et al. 2002). Elk are long-legged cursors, adapted to sustained running over uneven, open terrain to outdistance predators (Geist 2002).

Studies of wolf (*Canis lupus*)-ungulate systems have found that ungulates attempt to avoid high wolf density areas, especially during calving season, to reduce their risk of predation (Mech 1977, Edwards 1983, Stephens and Peterson 1984, Ferguson et al. 1988, Dekker et al. 1995), although Carbyn (1983) found equivocal relationships between elk and wolf distributions. Escape habitat that elk use when disturbed by predators include rivers, edges of cliffs, sloped terrain, tree cover, and human settlements (Cassirer et al. 1992, Dekker et al. 1995, Unsworth et al. 1998). Ungulates also use grouping (Hamilton 1971, Pulliam 1973, Dehn 1990, Hebblewhite and Pletscher 2002) or dispersion (Bergerud et al. 1984) to dilute wolf predation risk.

Predation risk can vary amongst individuals depending on age and body condition, shown in several studies in which wolves selectively kill old and young prey (Carbyn 1983, Kunkel et al. 1999, Smith et al. 2003b). Ungulates are particularly vulnerable to predation in high snow pack and during severe winters when snow conditions make locomotion difficult and forage inaccessible (Parker et al. 1984, Tefler and Kelsall 1984, Jédrzejewski et al. 1992, Huggard 1993, Mech et al. 2001). Some studies have suggested that ungulate avoidance of wolf

predation, whether accomplished by moving to low wolf density areas or spending more time vigilant, costs them foraging opportunities (Edwards 1983, Furguson et al. 1988, Laundré et al. 2001).

The reintroduction of wolves into Yellowstone National Park (YNP), Wyoming, in 1995 after a 70-year absence (Bangs and Fritts 1996) has been a major perturbation to the region and to elk in particular (Smith et al. 2003*b*). Before wolf reintroduction, predation upon elk calves by grizzly bears (*Ursos arctos*), black bears (*U. americanus*), and coyotes (*C. latrans*) accounted for nearly 90% of predator-caused mortalities and 40% of total mortalities of calves (Singer *et al.* 1997). In contrast, for adult elk, predation by grizzlies, coyotes, and cougars (*Felis concolor*) are minor sources of mortality, none of which are believed to substantially reduce the adult segment of the elk population (Murphy 1998, Knight et al. 1999, Crabtree and Sheldon 1999). As YNP's most abundant ungulate, elk now serve as a vital food source for wolves, constituting 92% of wolf kills (Smith et al. 2003*a*). Since reintroduction, the YNP wolf population has grown rapidly to 148 individuals as of 2002 (Smith et al. 2003*c*), yielding one of the highest wolf densities in the world at 50 wolves/1000 $km^2$ (Smith et al. 2003*b*). With wolves restored to the system, elk in Yellowstone now face substantially greater predation pressure, which could prompt them to alter their habitat selection patterns. To examine this possibility, I tested for differences in habitat selection by radiocollared elk before and after wolf reintroduction.

## STUDY AREA

Yellowstone National Park covers an area of 8991 $km^2$ in the northwest corner of Wyoming and on adjacent lands in Montana and Idaho. Elevation varies from 1500 to 3300 meters. Mean winter temperature ranges from -5 to -10°C, and mean summer temperature is between 13 and 18°C (Dirks and Martner 1982). At low elevations, precipitation averages 25 cm annually, 30-35% of which falls as snow. High elevations receive roughly 180 cm of precipitation per year, of which 70% is snow (Farnes et al. 1999).

The Northern Range spans the Lamar River and Yellowstone River watersheds and covers an area of 150,000 ha (Lemke et al. 1998). This area sits within the lower elevations of the park and adjacent land north of the park, where the climate is milder and drier than other regions of the park (Houston 1982). The vegetation is primarily steppe or shrub steppe (big sagebrush, *Artemisia tridentata*; Idaho fescue, *Festuca idahoensis*) with some stands of conifers (mostly Douglas-fir, *Pseudotsuga menziesii*) and aspen (*Populus tremuloides*) (Despain 1990).

Continuous conifer forests (Engelmann spruce, *Picea engelmannii*; subalpine fir, *Abies lasiocarpa*; lodgepole pine, *Pinus contorta*; whitebark pine, *Pinus albicaulis*) dominate the higher elevations on the Buffalo Plateau (north of the park) and in the interior and eastern portions of the park (Despain 1990) where the Northern Yellowstone elk herd summers (Houston 1982: 4).

In 1988, severe drought conditions led to extensive fires that burned 36% of YNP, the largest in the park's recorded history (Despain et al. 1989, Singer et

al. 1989). The fires briefly stimulated the protein levels and digestibility of forage, but within the first 2 years after the fires, elk did not show a preference for burned over unburned areas (Romme et al. 1995, Norland et al. 1996). However, secondary effects of the fires on elk habitat selection may emerge as successional changes in vegetation take place (Norland et al. 1996). Forested areas that were burned may show higher use by elk because of herbaceous understory growth (Singer and Harter 1996, Turner et al. 1999).

In the past 3-5 years, drought has prevailed again in the northern Rocky Mountains region of the U.S. (National Climatic Data Center 2003). Because drought adversely affects forage production (Farnes et al. 1999), dry conditions could drive elk to use higher elevations that receive relatively more precipitation.

Other large mammals inhabiting YNP besides elk and wolves include bison (*Bison bison*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), grizzly bears, black bears, coyotes, and cougars (YNP 1997).

## METHODS

### Data Collection

We used helicopter net-gunning to capture adult cow elk in the winters of 2000-2002. Each elk was fitted with a VHF radiocollar equipped with a mortality beacon. We targeted elk distributed throughout the Northern Range to ensure good representation of the herd, although we did not capture outside of park

boundaries. Using aerial telemetry from a Supercub airplane, we attempted to locate each individual once per week. This analysis includes postwolf-reintroduction data collected between 21 June 2000 and 1 November 2002, comprising 3 summers and 2 winter seasons. Universal Transverse Mercator (UTM) locations were taken in North American Datum 1983 (NAD83) using a Garmin GPS unit. When marking the position, all attempts were made to visually identify the collared animal, or at least its group. Error associated with aerial telemetry locations (White and Garrott 1990) was assessed in 27 non-visual relocation trials and 18 visual relocation trails. For non-visual trials, the pilot located a hidden radiocollar based solely on the radiosignal. Visual trials involved locating a collar placed on a 30 x 30 $in^2$ florescent orange mat, giving the pilot both the radiosignal and a visual cue with which to determine a location. Also we opportunistically measured telemetry error whenever we aerially located a dead collared elk or a dropped collar.

For comparison to the present-day elk location data, I used prewolf locations of radiocollared cow elk monitored aerially from January 1985 – April 1987 (7 cows, J. M. Vore) and January 1987 – April 1990 (21 cows, F.J. Singer and D.J. Vales). The first set of cows was captured in 1985 and 1986 in the Stephens Creek and Eagle Creek areas of the Lower Northern Range using clover traps for a study examining movements and distribution of elk relative to hunting zones (Vore 1990). Only those cows that migrated into the park were used in this analysis for comparison to the current sample of cows captured within the park. Additional cows were captured for a separate study in 1987 using clover traps

placed in the middle and upper sections of the Northern Range (Vales and Peek 1996, Harting and Singer 1988). These data were sub-sampled to eliminate consecutive locations for individuals that occurred <5 days apart. In addition, because 2 herd segments (Gallatins and Buffalo Plateau) were not well-represented in the prewolf cow elk data, radiocollared calf locations from 1987-1990 (66 calves total, 65 having summer data, 39 with winter data; Singer et al. 1997, Smith et al. 1998) were used as a substitute for cow locations. Only those calves that survived their first summer and/or first winter were included in the analysis to minimize potential bias in habitat selection by mortality-prone calves. Consecutive calf locations spaced <5 to 7 days apart were discarded. All prewolf locations were distinguished as either pre-fire or post-fire, based on the date of the location relative to the date of the nearest burn that occurred in the 1988 fires. Most of these locations were taken using aerial telemetry. However, telemetry error was not measured during the prewolf period.

The season for each location was designated as summer, winter, or migration, based on whether the elk was on its summer home range (i.e., not on the Northern Range), winter home range (i.e., on the Northern Range), or in between. The summer and winter locations of 6 non-migratory elk that summered on or near the Northern Range were distinguished using the median dates of transition between summer and winter ranges shown by the migratory elk. Spring migration generally occurred in late May and fall migration occurred in mid-October to early November (see Evans 2003 for more details on migration). Elk locations taken during migration periods were not used in the habitat selection

analysis. All locations were recorded during daylight hours, usually between 0700 and 1300. This analysis therefore only discusses habitat selection by elk during these times of the day.

**Habitat Availability**

The spatial extent of habitat available to individuals was defined by seasonal herd segment areas. Houston (1982:34) described herd segments as "elk with similar affinities for specific range areas and similar patterns of movement in response to changing environmental conditions." A fairly large extent of >10 km diameter, such as the area of a seasonal herd segment, is necessary to capture the variability in landscape features of YNP (Boyce et al., in press) and encompasses the area over which an elk would reasonably travel between successive relocations taken at approximately a weekly interval.

I did not consider a larger extent than the herd segment because elk show strong fidelity to their home ranges (Craighead et al. 1972, Shoesmith 1979), so selection of a herd segment area from the available parkwide landscape is likely to be dictated more by learned migration routes and familial associations (Shoesmith 1979) than by resources and habitat types. In addition, because there were insufficient locations per elk to adequately define individual home ranges (≥50 locations per animal, Leban et al. 2001), I could not pursue analysis at a smaller extent than the herd segment.

To define herd segments, I grouped elk locations into several geographic regions. Summer elk locations were assigned to one of 5 herd segments based on

similarities in migration routes and geographic summer ranges (Evans 2003). Winter elk locations were partitioned into 4 regions of the Northern Range delineated by topographic features (e.g., river canyons and mountain ranges) and similarities in distributions amongst individuals. Using these groups of elk locations, I calculated 95% kernel polygons for summer herd segment areas and winter Northern Range sections (Figures 1 and 2). Elk locations falling outside of the kernels were discarded from further analysis.

I assumed that each elk had *a priori* knowledge of its portion of the summer or winter range, and that it could travel throughout its area within the time elapsed between relocations. Random points (20 per summer elk point, 13 per winter elk point), representing locations available to elk, were generated within these polygons and were matched to corresponding elk locations spatially (within each polygon) and temporally (by season and also within seasons by time-specific GIS layers: see below).

**Habitat Characteristics**

I used geographic information system (GIS) coverages of vegetation type, habitat openness, elevation, slope, wolf density index, and snow water equivalent (SWE: Farnes and Romme 1993) to obtain data on habitat characteristics at used and available locations (Tables 1 and 2). Two vegetation maps, representing pre-1988 and post-1988-fire conditions, were used (Dixon 1997, Mattson et al. 1999). For mosaic vegetation pixels (i.e., >1 vegetation type), I randomly chose 1 of the first 2 listed vegetation types. I then consolidated the vegetation types into broad

categories: grasslands, shrublands, other nonforest (rock, talus, lithic ridges, streams and ponds, etc.), burned conifer, unburned conifer, and aspen. Willow (*Salix* spp.) habitat was not well mapped on the Northern Range, so it could not be considered as a separate vegetation type and instead was included in the shrublands category (Mattson et al. 1999). Habitat openness was calculated for each grid cell as the percentage of nonforested pixels within a 400-m radius, the median flight distance at which YNP elk reacted to human disturbance (Cassirer et al. 1992). Elevation was taken from a 30-m Digital Elevation Map (DEM), and slope in degrees was derived from the DEM.

Wolf density index maps, represented by kernel utilization distributions (Worton 1989, Hooge and Eichenlaub 1997), were made using weekly radiolocation data of collared wolves. Wolf locations were obtained from the Yellowstone Wolf Project, which maintained radiocollars on 27%, 34%, and 25% (32, 45, and 37 wolves) of the YNP wolf population in 2000, 2001, and 2002 (Smith et al. 2001, 2003*c*; Smith and Guernsey 2002). Collars were distributed among wolf packs in proportion to pack size, so that wolf radiolocations were representative of the distribution of the YNP wolf population (D. W. Smith, National Park Service, personal communication).

The wolf density index is a unitless measure of relative wolf predation risk. Separate wolf maps were made for early (May-June), mid (July-August), and late (September-October) summer, and winter (November-April) for each year (2000-2002) (Figure 3). The index was calculated for each pixel as:

$$\text{Wolf density index} = (101 - \text{Kernel value}) * N_w/10,$$

where $N_w$ is the number of wolves on the landscape (69, 90, and 88 adult wolves in early and mid-summers 2000-2002; 126, 139, and 158 adults and pups in late summers 2000-2002 and winters 2000/2001 and 2001/2002). This factor adjusts the wolf density index to account for (1) annual variation in wolf population size and (2) seasonal variation in wolf distribution and movements while pups develop from non-hunting dependents in early and mid-summer into more active predators in late summer and winter. The wolf density index ranges from low (6.9) to high (1580) values, representing a maximum wolf density of 50 wolves/1000 $km^2$ on the Northern Range in winter (Smith et al. 2003*b*).

Snow maps, measuring SWE (cm), were made using the Yellowstone snow model developed by the Natural Resources Ecology Lab at Colorado State University (Wockner et al. 2002). A snow map was made for each day on which the cumulative change in SWE at either the Mammoth, Tower Falls, or Lamar snow stations since the previously mapped snow day was ≥1.2 cm. Farnes et al. (1999) estimated that accumulations of 2.5 to 5.0 cm of SWE can prompt elk to move to areas of lower snow, so snow maps made at an interval of <2.5 cm of SWE should be sufficient to detect responses of elk to changes in SWE.

To assess moisture/drought conditions during the forage growing season, I calculated the mean Keetch-Byram Drought Index (KBDI: Farnes et al. 1999) values for the first 750 Growing Degree-Days (GDD) of each year. Most forage production occurs during these first 750 GDD (Farnes et al. 1999). I averaged the KBDI within each of 5 weather stations distributed throughout the elk summer range (Tower Falls, Canyon, Yellowstone Lake, Parker Peak, and Old Faithful)

and then took the mean of these values across stations but within years. I compared the mean KBDI for each year with the 1961-1990 mean KBDI for these stations reported by Farnes et al. (1999) using paired *t*-tests. 1988, 2000, and 2001 were expected to be drought years. KBDI data were not available for summer 2002, so moisture levels for this growing season could not be assessed.

**Habitat Selection Models**

Prewolf and postwolf-reintroduction models of habitat selection were built by comparing used and available habitats to obtain Resource Selection Functions (RSF) (Manly et al. 2002). RSFs are equations that predict the relative probability of use, taking the form:

$$w(X) = \exp(\beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n),$$

where $w(X)$ is the RSF value, $\beta_i$ are the estimated coefficients, and $X_i$ are the habitat variables (Manly et al. 2002).

To estimate the $\beta_i$s, I used conditional fixed-effects logistic regression, also called, discrete choice, matched case-control, McFadden's choice, or paired logistic regression (StataCorp 2001:200-215). Conditional fixed-effects logistic regression allows one to account for differing availabilities of habitats amongst observations by matching used locations to a "choice set" of random locations (Arthur et al. 1996, McCracken et al. 1998, Cooper and Millspaugh 1999, Compton et al. 2002). Choice sets are specific to the individual and to the space and time at which the individual was observed (McCracken et al. 1998). In this analysis, conditional fixed-effects logistic regression ensured that changes in

vegetation following the 1988 fires, and variation in wolf distribution and snowfall by year and season were taken into account when comparing used with available habitat. I grouped used locations by

1. elk and vegetation map for the prewolf summer data (≤2 time periods/elk),
2. elk and wolf map for the postwolf summer data (≤10 time periods/elk),
3. elk, vegetation map, and snow map for the prewolf winter data (≤39 time periods/elk), and
4. elk, wolf map, and snow map for the postwolf winter data (≤42 time periods/elk).

I used the corrected Akaike information criterion ($AIC_c$: Burnham and Anderson 1998) to rank *a priori* candidate models (Tables 3 and 4). Candidate models were chosen to evaluate the alternative hypotheses that

1. elk select habitat based on vegetation type, habitat openness, snow, elevation, and/or slope,
2. elk avoid wolves, in addition to selecting for other habitat characteristics, and
3. avoidance of wolves by elk is tempered by their selection for other habitat characteristics.

I only considered linear interactions between the wolf density index and the other continuous variables. Because of collinearity in the postwolf dataset between elevation and SWE ($r = 0.62$), elevation was not included as a predictor in the winter models.

I conducted *post hoc* exploration to refine the top *a priori* models. When a quadratic relationship between the logit of the RSF and a predictor variable gave an optimum that fell near or beyond the range of possible values of a predictor variable, I tested whether a linear term would provide a better fit (based on $AIC_c$) than including the additional squared term. I also examined whether some interaction terms could be discarded from the *a priori* models (Anderson and Burnham 2002). Models were evaluated through *k*-fold cross-validation, using Spearman's rank correlation coefficient (rho) as the test statistic ($k = 5$, $n = 10$) (Boyce et al. 2002, Boyce et al., in press).

I report 3 models for each season: the highest scoring prewolf and postwolf models that have the same predictor variables ("non-wolf" [NW] models without the wolf density index term, henceforth called "prewolf" and "postwolf-NW" models), and the top-ranking postwolf model that includes the wolf density index term (full "postwolf-W" model). I assessed changes in habitat selection between the prewolf and postwolf time periods by comparing the $\beta_i$ coefficients between the "non-wolf" models for each predictor variable. For linear relationships, I tested for differences in $\beta_i$s using a *t*-test (Brown and Rothery 1993:227). For quadratic relationships, I tested for differences in optimal values between the pre-wolf and post-wolf models using a *Z*-test, assuming a Gaussian distribution around each optimum. The optimal value for a predictor variable $X$ based on setting the first derivative of the regression equation with respect to $X$ equal to 0 is:

$$X_{max} = \frac{-\beta_1}{2\beta_2},$$

where $X_{max}$ is the optimum, $\beta_1$ is the estimated coefficient for the linear term, and $\beta_2$ is the estimated coefficient for the squared term. The SE for $X_{max}$ was calculated using error propagation of the SEs of the $\beta_i$s (Stuart and Ord 1994:351, eq. 10.17):

$$SE(X_{max}) = |X_{max}| * \sqrt{\left(\frac{\sigma_{\beta_1}}{\beta_1}\right)^2 + \left(\frac{\sigma_{\beta_2}}{\beta_2}\right)^2 - \left(\frac{2}{\beta_1\beta_2}\right) * \mathrm{cov}(\beta_1, \beta_2)}\,.$$

Finally, I examined the postwolf-W model to describe relative distributions of elk and wolves and selection of habitat components by elk in varying relative wolf densities.

**RESULTS**

Ninety-three adult cow elk were captured and radiocollared: 45 in March 2000, 28 in February 2001, and 20 in February 2002. Thirteen elk were excluded from analysis because they died within 2 weeks after capture, had collar malfunctions that did not permit radiotracking, or otherwise had few (<7) relocations. The remaining 80 elk were each relocated an average of 12 times/season/year (SE = 0.26), yielding 1560 summer and 1590 winter locations. The mean time interval between successive locations for an individual was 12 days (SE = 0.11). In 69% of summer and 65% of winter locations, the collared elk was visually identified (a "visual" location; estimated error = 24 m (SE = 4)). In 16% of summer and 32% of winter locations, the collared elk's group was located, but the collared elk itself was not discerned (error was not measured for this type of location, but was likely intermediate to the visual and non-visual

errors). Neither the collared individual nor its group was seen in 15% of summer and 3% of winter locations ("non-visual" locations; estimated error = 86 m (SE = 13)).

The prewolf data consisted of 431 summer locations and 738 winter locations of radiocollared cows, and 724 summer locations and 322 winter locations of radiocollared calves. Preliminary analysis showed that there was no difference in models derived from prewolf cow data only, calf data only, or the combined prewolf cow + calf data, thus justifying the use of calf locations as a proxy for cow locations.

Based on mean KBDI, the first 750 GDD of 1985-1987, 1989, and 2000 were similar to the long-term average moisture levels (Table 3). The growing season of 1988, the year in which the massive fires occurred, was drier that the long-term average, whereas that of 2001 was wetter than the long-term average (Table 3).

**Summer Habitat Selection Models**

*Model Selection*.-- The best *a priori* summer models based on $AIC_c$ were the full models which included terms for vegetation types, elevation, habitat openness, and slope in the NW models and additional terms for wolf density and interactions between wolf density and elevation, openness, and slope in the W model (Table 4). The *a priori* prewolf model #NW-4, which had both a linear and squared term for habitat openness, predicted maximum selection for habitat openness of 95%, whereas its postwolf counterpart predicted a maximum at 2%

openness, suggesting that linear terms could be sufficient. When I then conducted *post hoc* refinement of the best *a priori* models, I found that using only the linear term for openness made a large improvement on the prewolf model #NW-4 based on AICc, although only a minor improvement on the postwolf model #NW-4 (Table 6). Modifying the best *a priori* postwolf-W model, #W-4i, I found that using a linear wolf density term and only including one interaction term, *slope*wolf density*, made a negligible improvement (Table 6). Although only 1 of these *post hoc* models greatly improved on its matching *a priori* model, I selected all 3 *post hoc* models as the overall best summer models based on the principle of parsimony.

The selected prewolf and postwolf-NW summer models predicted elk use based on vegetation, a linear relationship with habitat openness, and quadratic relationships with elevation and slope (Table 6). The selected postwolf-W model included a negative linear wolf density term and a negative interaction between slope and wolf density (Table 6). All of the models predicted well, according to *k*-fold cross validation (Table 6).

*Prewolf and postwolf model comparisons.*-- Elk selected for less open habitats in summer during the postwolf period compared to prewolf ($t = -7.79$, $P < 0.01$). Specifically, elk showed greater selection for burned forest (relative to grasslands) after versus before wolf reintroduction ($t = 5.72$, $P < 0.01$). Elk selected for higher elevation postwolf (optimum at 3434 m [SE = 184.4]) than prewolf (optimum at 2451 m [SE = 19.7]) ($Z = 5.30$, $P < 0.01$). The optimal elevation in the postwolf models falls beyond the range of actual elevations in

YNP (maximum elevation available = 3334 m, maximum elevation used by radiocollared elk = 3190 m), so the partial RSF with respect to elevation monotonically increases within the possible range of elevations. The optimal slope in the postwolf-NW model (8 degrees [SE = 2.2]) did not differ from that of the prewolf model (3 degrees [SE = 3.5]) ($Z = 1.02$, $P > 0.05$). However, the postwolf-W model had a significant positive interaction between slope and wolf density index (Table 6, Figure 4). Elk also selected for low wolf density areas, shown by the negative β for wolf density index (Table 6).

**Winter Habitat Selection Models**

*Model Selection*.-- The best *a priori* winter models were full models that included terms for vegetation, SWE, openness, and slope in the NW models and additional wolf density and interaction terms in the W model (Table 5). No *post hoc* refinement was needed for the prewolf and postwolf-NW models (Table 7). Modifying the structure of the postwolf model #W-2i, I generated a *post hoc* version that lacked the *openness*wolf density* interaction term (Table 7). Although this *post hoc* model only improved the $AIC_c$ score by a fraction, I chose this model because it was more parsimonious than the *a priori* model.

The selected winter prewolf and postwolf-NW models predicted elk use based on vegetation, quadratic relationships with habitat openness and slope, and a negative linear relationship with snow (Table 7). The selected postwolf-W model included a quadratic relationship with wolf density and negative

interactions with slope and snow (Table 7). *K*-fold cross validation showed that all of these models predicted well (Table 6).

*Prewolf and postwolf model comparisons*.-- Elk selected for more open habitat in winter, postwolf (optimum at 71% openness [SE = 3.4]) compared to prewolf (optimum at 57% openness [SE = 1.4]) ($Z = 3.72$, $P < 0.01$). Relative to selection for grasslands, selection for shrublands ($t = -2.12$, $P < 0.05$) and other nonforested habitat ($t = -2.05$, $P < 0.05$) was lower postwolf versus prewolf. There was no difference in the effect of snow between the two time periods ($t = 0.36$, $P > 0.05$); in both cases, elk selected for low SWE (Table 7). Selection of slope did not differ ($Z = 0.25$, $P > 0.05$); in both time periods, elk selected an optimum of 9 degrees slope (SE = 2.2, prewolf; SE = 0.9, postwolf). In the postwolf-W model, the optimal wolf density index (given median available values of 12 degrees slope and 4.4 cm SWE: Table 2) was 994. Negative interactions in selection coefficients were found between slope and wolf density and between snow and wolf density (Table 7, Figures 5 and 6).

## DISCUSSION

Habitat selection patterns by the Northern Yellowstone elk herd changed between 1985-1990 and 2000-2002. Aside from effects due to wolves, some of these changes may be a result of post-fire succession and other environmental factors. In fact, wolves, fire, and climate likely interact to affect prey behavior and fitness (Carbyn 1983, Jédrzejewski et al. 1992, Huggard 1993, Kunkel and Pletscher 2001, Mech et al. 2001). At the weekly temporal resolution of this

study, elk avoided high wolf density areas in summer. However, in winter elk selected for areas of moderately high wolf density; i.e., they were unable to spatially separate themselves from wolves, indicating that winter habitat selection by wolves more closely mirrored habitat selection by elk at this scale. Instead, any avoidance of wolves in winter must take place on a smaller timeframe, e.g., an encounter-by-encounter basis (see MacNulty 2002 for details on wolf-elk encounters and attacks in YNP).

**Changes in Summer Habitat Selection**

Elk have shifted toward selection for less open habitats, specifically more burned forest, in summer. Contrary to the notion that predator avoidance comes at the cost of foraging (Lima and Dill 1990), elk in YNP may benefit in both respects by selecting burned forest habitats. Herbaceous understory has increased in burned forests following opening of the canopy by fire (Turner et al. 1999), so elk may be making use of the available forage. Present-day selection for burned forest (12 to 14 years after the 1988 fires) contrasts with the earlier finding by Norland et al. (1996) that within the first 2 years postfire, no change in summertime habitat selection occurred. However, as those authors predicted, changes in habitat selection did occur later as long-term succession of burned forests began to take place.

Furthermore, unlike elk, wolves in Yellowstone avoid burned forest (Yellowstone Wolf Project, unpublished data). Burned forests in YNP are characterized by substantial downfall (Tinker and Knight 2000), which can be an

obstacle to locomotion (Parker et al. 1984). Wolves search for prey by traveling long distances and making chance encounters (Mech 1970). Usually they must run down their prey (Mech 1970), so chasing an elk through downfall could prove challenging. Overall, it may be energetically unprofitable for wolves to travel and hunt in burned forest. Elk, on the other hand, may use the complex habitat structure of downed timber and young regenerating lodgepole pines for hiding cover. This contrasts with the hypothesis given by Kunkel and Pletscher (2001) that understory vegetation is disadvantageous to prey because wolves use such vegetation as stalking cover when they hunt in Glacier National Park. The discrepancy could be attributable to the vast extent of burned forest in Yellowstone and differences in the habitat structures of the 2 parks.

In addition, if an elk does encounter wolves in burned forest, it may be able to defend itself using downed timber against which to back up and protect its flanks and rear, leaving its front hooves prepared to kick, if attacked. On the Northern Range (N. Varley, University of Alberta, personal communication) and in Jasper National Park, Alberta (Schmidt and Gunson 1985, Dekker et al. 1995), elk have been observed backing up against a tree or the edge of a cliff to block wolves from attacking from behind. Wolves are less successful at attacking a prey that stands its ground, for fear of injury due to kicking (Mech 1970, MacNulty 2002). MacNulty (2002) found that elk in YNP stand to defend themselves in over 50% of encounters with wolves, mostly recorded in winter, but it is not well-known how elk respond to wolf encounters in the summer under a very different climate and habitat regime, nor is it known how elk explicitly react

to predators in burned forest habitat. Nevertheless, by choosing habitat that wolves do not favor, elk can reduce their rate of encounter with wolves.

Elk have shifted to selection for higher summer elevations postwolf compared to prewolf. Drought did not appear to be a factor causing elk to select higher elevations postwolf. The summer growing seasons of 2000 and 2001 were similar in moisture to or wetter than the prewolf summers 1985-1989. Nevertheless, with much of the summer range converted into burned forest, which lacks canopy cover to shade the understory, summer forage may dry faster currently than before the 1988 fires. A change in plant phenology resulting indirectly from the fires could drive elk to higher elevations in search of moister forage and cooler temperatures.

Movements to higher elevation in summer also allow elk to reduce their encounter rate with wolves during the pup-rearing season. Wolves in YNP den at lower elevations in April while the elk herd is still on the Northern Range (Thurston 2002). However, elk leave the Northern Range and migrate to the summer range beginning in mid-May (Craighead et al. 1972, Evans 2003). Between May and August, although adult wolves may travel widely to hunt, they must to return to the dens and rendezvous sites to feed the pups (Mech 1970, Thurston 2002). Elk that summer at higher elevations distance themselves from wolf activity centers, thus reducing their predation risk (e.g., Bergerud et al. 1984).

**Changes in Winter Habitat Selection**

In contrast to summer, elk have shifted to wintertime selection for more open habitats following wolf reintroduction. Because wolf density within YNP is highest on the Northern Range (Smith et al. 2003*b*), the wolf predation risk that elk experience is higher in winter than summer. Elk were unable to avoid wolves in winter on the week-to-week basis on which data were collected in this study. One possibility is that on the largely nonforested landscape of the Northern Range, now that wolves have been restored to the system, more elk may be using grouping as an anti-predator strategy (Dehn 1990, Jédrzejewski et al. 1992, Hebblewhite and Pletscher 2002). Group size data associated with radiocollared elk were not collected during the prewolf period, so a comparison of grouping before and after wolf reintroduction was not possible. However, within the postwolf period, elk group sizes were larger in higher wolf density areas, even after accounting for vegetation cover (Appendix A). Of course, larger groups attract more wolves (Hebblewhite and Pletscher 2002), and elk may form groups for reasons other than predation risk, such as patchiness of available forage (Heard 1992, Clarke et al. 1995) and social interaction (Franklin and Lieb 1979, Shoesmith 1979, Bender 1996). Regardless of the immediate mechanism causing elk to aggregate, grouping allows elk to (1) dilute wolf predation risk, essentially using their fellow group members as hiding cover (Hamilton 1971), and (2) detect approaching wolves more readily, given more eyes watching (Pulliam 1973). In very large groups, such as the aggregations of as many as 700 elk that I observed, the dilution effect plays a more important role than detection in reducing per

capita predation risk (Dehn 1990). Elk can capitalize on this strategy on the open landscape of the Northern Range where they otherwise cannot use dispersion or tree cover for hiding.

Trophic cascades promoting willow and aspen growth (Romme et al. 1995, Singer et al. 1998, Ripple et al. 2001, White et al. 2003) could result from a reduction in the elk population by wolves (e.g., Boyce 1993) or from distributional shifts and increased movements of elk avoiding wolves (e.g., Mitchell and Lima 2002). However, in this study elk showed no significant change in selection for aspen, which was highly preferred in both prewolf and postwolf periods during winter. After wolf reintroduction, elk showed decreased selection for shrublands relative to grasslands. The shrublands category includes willow, but because willow is not well mapped on the Northern Range, selection of willow could not be measured. Furthermore, very low elk density (e.g., 3 elk/km$^2$) may be required to see a substantial release of herbivory on these species (White and Feller 2001). With elk density on the order of 10 elk/km$^2$ (Lemke et al. 1998) and YNP wolf population beginning to level off (Smith et al. 2003*b*), wolves alone may not be able to alter elk demography and herbivory patterns to achieve willow and aspen release. Other factors including fire, precipitation, and beaver activity might interact with wolf predation on elk to enhance growth of willow and aspen (Romme et al. 1995, Baker et al. 1997, Singer et al. 1998, Ripple and Larsen 2000).

**Interactions between Selection of Wolf Density and Other Habitat Features**

Although there were no overall differences in selection of slope or SWE before versus after wolf reintroduction, selection of these habitat features did vary depending on wolf density. Elk avoided wolves in summer, but those elk that did occur in high wolf density areas selected for steeper slopes. Using sloped terrain gives an ungulate a better vantage from which to watch for predators (Byers 1997, Kunkel and Pletscher 2001). Wolves (Carroll et al. 2003) and wolf kills (Bibikov 1982, Kunkel and Pletscher 2001) tend to occur in lower sloped habitat, suggesting that ungulates are easier to kill on shallow slopes. Having a higher center of gravity than wolves, ungulates may be more likely to stumble if they run downslope and they may lose momentum once reaching the bottom of a hill (Bibikov 1982). In contrast, ungulates that move upslope are less likely to be attacked by wolves because they may be in a better position to defend themselves by kicking downward, or because wolves may be able to detect that prey that are fit enough to climb a slope would be difficult to kill (Bibikov 1982). Cassirer et al. (1992) reported that a common response of elk to disturbance by skiers was to move upslope onto ridges. Elk probably respond in a similar manner when disturbed by wolves and other predators. Although almost none of our radiolocations of elk occurred during actual encounters with wolves, a higher encounter rate in areas of high wolf density could result in the observation of elk selecting steeper slopes in those places.

In the winter, elk that were in higher wolf density areas selected for lower slope, contrasting with the summertime. This finding is unlikely to be an anti-

predator strategy and instead points to the greater predation risk elk face in winter. On a weekly timescale elk could not avoid wolves, so selection of low slope in winter coinciding with high wolf density may reflect the similarities in habitat selection by elk and wolves at this scale (e.g., Kunkel and Pletscher 2001), rather than avoidance strategies by elk.

Elk also selected for lower SWE in higher wolf density areas. Most large mammals, elk and wolves included, prefer areas of low snow accumulation for ease of locomotion (Tefler and Kelsall 1979, Houston 1982:139, Parker et al. 1984, Kunkel and Pletscher 2001, Slovkin et al. 2002). Deep and crusted snow is a hindrance to both movement and foraging for grazers (Tefler and Kelsall 1979), but can be beneficial to wolves, which enjoy a higher kill rate under such conditions (Nelson and Mech 1986, Mech et al. 2001, Smith et al. 2003a). This suggests that the probability of an elk being killed is greater in deeper snow than shallow snow, so although elk may contend with a high rate of encounter with wolves in low snow areas, their probability of capture should be lower where movement is easier and where flight and defense are both available options. Prey can tolerate risky habitats if their probability of escape outweighs the probabilities of encounter and attack (Lima 1992).

**Trade-offs and Seasonal Strategies of Habitat Selection**

The ability of elk to avoid wolves by using habitat selection is seasonally dependent in YNP, largely because of the migratory nature of the Northern herd and their use of vastly different summer and winter ranges. Because each

seasonal range presents elk with different availabilities of habitats and resources from which to choose, elk show different responses to wolf predation risk between the 2 seasons.

On the summer range, where forage is abundant, elk have the luxury of choosing habitats that allow them to avoid wolf predation. As discussed previously, elk do not always need to make a trade-off between food and safety. Elk disperse throughout an expansive summer range, and they can avoid wolves by choosing particular habitat structures and terrain features that reduce their risk of wolf predation.

In winter, however, in addition to high wolf density, elk face severe weather conditions, greater competition due to higher density, less nutritious forage, and loss of fat reserves and body weight (Houston 1982, Cook 2002). In fact, mortality during winter accounts for nearly all of the annual cow elk mortality in this herd (Evans 2003). Winter is a time of subsistence feeding at best, so elk may choose not to trade foraging for spatial avoidance of wolves and instead wait until a wolf encounter occurs to expend energy avoiding predation. Those elk that are in better physical condition are less likely to be killed because they are more fit to either outrun wolves or successfully confront and aggressively fend them off (MacNulty 2002, Smith et al. 2003a). One way that elk could enhance their probability of surviving the winter is to consume high-quality forage during summertime to build fat reserves that allow them to enter the winter in good physical condition (Cook 2002).

## MANAGEMENT IMPLICATIONS

As wolf populations expand throughout the Rocky Mountains, I expect that in areas where elk are the primary prey of wolves, elk will show changes in distribution and habitat selection. Some are concerned that wolf predation may be reducing the Northern Yellowstone elk population at the expense of hunting opportunities for humans (Montana Fish, Wildlife and Parks 2003), but it may be that elk are simply more difficult to hunt because they have shifted to selection of more forested habitat (this study) and are more vigilant where they are exposed to wolf predation (Laundré et al. 2001, Wolff and Van Horn 2003). In elk populations that are at lower density than the Northern Yellowstone herd or where more hiding cover or escape terrain is available than on the Northern Range, elk may be able to employ habitat selection in both summer and winter to avoid wolves. Large and diverse habitats are important for maintaining a predator-prey system by giving prey more escape cover (Huffaker et al. 1963, Pimentel et al. 1963, Taylor and Pekins 1991). Complexity of habitat structure, achieved through such means as fire and succession, along with a large forage base, such as the summer range in this study, can contribute to the persistence of elk populations under wolf predation pressure.

**APPENDIX A. Elk group sizes relative to wolf predation risk and habitat structure in Yellowstone National Park, Wyoming**

Group formation is a widespread behavior found in many prey species (Allee 1931, Slobodchikoff 1988). Aggregation could occur simply because of the underlying distribution of food and other resources or to facilitate breeding, but grouping behavior is also thought to have an anti-predatory function (reviewed in Bertram 1978). By joining a group, an animal can dilute its probability of being preyed upon because individuals in larger groups should experience a lower per capita rate of capture than those in smaller groups (Hamilton 1971). Animals further benefit from grouping because larger groups can detect a predator more readily through collective vigilance (Pulliam 1973). The individual animal benefits because it can allocate less time to vigilance and more time to feeding (Elgar 1989). Combining the dilution and detection effects, Dehn (1990) predicted that as group size increases, the dilution effect should play an increasingly important role in anti-predatory behavior relative to the detection effect.

Competition for resources among group members heightens with increasing group size, suggesting that an optimal group size exists at which the costs and benefits of group living are balanced and the fitness of individuals in the group is maximized (Bertram 1978). Observed group sizes are usually larger than this optimum, however (Silby 1983, Pulliam and Caraco 1984), and can persist as long as the fitness of individuals in a group is greater than the fitness of a solitary

individual (Sibly 1983, Giraldeau and Gillis 1985, Kramer 1985). In species in which individuals are free to intermingle and are not strictly bound by territoriality, kinship, or other behavioral constraints, fluidity in group size is expected as groups encounter one another and redistribute group membership to maximize individual fitness.

Elk (*Cervus elaphus*) are social ungulates, evolutionarily adapted to living in open plains (Geist 2002). Grouping serves as an anti-predatory strategy suited for such animals living in predominantly open habitats (Geist 2002), in contrast to the more solitary strategy of the moose (*Alces alces*), typically a forest-dwelling ungulate (Molvar and Bowyer 1994). Individual elk show low fidelity to each other beyond the basic social unit of a cow and calf (and sometimes a yearling), such that interchange of cow-calf units among groups is common (Shoesmith 1979). Group sizes of the Northern Yellowstone elk herd, recently reintroduced to its most important natural predator, the wolf (*Canis lupus*) (Bangs and Fritts 1996), are predicted to vary seasonally and to be larger in areas of higher wolf density and lower hiding cover.

*Predictions of seasonal variation in elk group sizes*

Elk form large groups in the summer and winter, punctuated by declines in group size during calving and rut (Knight 1970, Franklin and Lieb 1979, Houston 1982, Jenkins and Starkey 1982, Bender and Haufler 1999). Smallest group sizes are seen during calving in mid-May to June because parturient females use a hider strategy to conceal newborn calves, moving away from the main herd to give birth

in seclusion (Geist 2002). Not until the calves are 1-3 weeks old do mothers and calves rejoin the main groups, leading to larger groups in mid-summer (Franklin and Lieb 1979).

During rut, group sizes drop typically to under 20 animals, limited by the number of cows a bull can herd (Altmann 1956). Group sizes during rut are also inversely related to the bull:cow ratio in the population due to competition among males (Bender 1996). In systems that receive heavy snowfall, larger winter groups form in part because habitable space and forage become more limiting and more patchily distributed as snow accumulates (Heard 1992). The Northern Yellowstone herd concentrates in the winter onto an area roughly one sixth the size of its summer range (Houston 1982), so larger winter groups occur in part because of increased density.

Population density also could be responsible for regional differences in group size. In the Pacific Northwest, northern California, Michigan, and Banff National Park, group sizes reach a maximum of roughly 30 animals (Franklin and Lieb 1979, Jenkins and Starkey 1982, Bender and Haufler 1999, Hebblewhite and Pletscher 2002), whereas in Montana and Wyoming, which hold the highest densities of elk in North America, group sizes are frequently >50 and can seasonally number in the hundreds (Knight 1970, Houston 1982).

*Predictions of elk group sizes relative to wolf density*

Studies of other ungulates show that larger groups occur in the presence of higher wolf density (white-tailed deer [*Odocoileus virginianus*]: Nelson and Mech

1981; musk-oxen [*Ovibos moschatus*]: Heard 1992). In Banff National Park, where elk density is 2.5 elk/km$^2$, wolves are more likely to encounter and make a kill in a larger group of elk (>30 animals), but the probability of an individual elk being captured was greatest for animals in intermediate-sized groups of 13-30 individuals (Hebblewhite and Pletscher 2002). Hebblewhite and Pletscher (2002) suggested that elk should adopt a bimodal strategy of either remaining alone or in small groups to avoid detection by wolves, or aggregating in large groups to maintain a high level of group vigilance and to dilute the probability of being captured in the event of an attack. In Yellowstone, elk population density is higher at 10 elk/km$^2$ (Lemke et al. 1998), and groups of hundreds commonly occur in Yellowstone (Houston 1982). Because the dilution effect is particularly important at high densities (Dehn 1990), cow elk in Yellowstone are expected to adopt the latter strategy, forming larger groups in response to heightened predation risk.

*Predictions of elk group sizes relative to habitat openness*

In open habitats, large prey animals are highly visible to predators, but by forming groups, prey can use members of their own species as hiding cover (Hamilton 1971). In the Sun River herd of Montana, the largest groups of elk were found on open grass and valley bottom vegetation types (Knight 1970). Similarly red deer on the island of Rhum, Scotland, formed the largest groups on grassy areas and smallest groups in shrubby heather moorlands (Clutton-Brock et al. 1982). As an exception, in Michigan elk group size did not vary inversely with

vegetative cover, but this population has not been subject to year-round nonhuman predation for >70 years (Bender and Haufler 1996). These elk might not receive the typical anti-predator benefits of grouping, leading to a decline in the tendancy to form larger groups in more open habitats (Bender and Haufler 1996). In Yellowstone, where elk are now subject to wolf predation, group size is expected to increase with habitat openness.

## METHODS

### Study area

Yellowstone National Park (8,991 $km^2$) is located in northwest Wyoming and on adjacent areas of Montana and Idaho. Yellowstone's long, cold winters with heavy snowfall at higher elevations drive the Northern Yellowstone elk herd to migrate between higher elevations of the park in summer and the low elevation wintering grounds on the park's Northern Range (Houston 1982, Evans 2003). The 1,530 $km^2$ Northern Range is a mostly nonforested landscape, whereas the summer range, which spans most areas of the park, is primarily forested (Despain 1990). Wolves were reintroduced to Yellowstone in 1995 (Bangs and Fritts 1996) and their population has grown rapidly to 132 individuals within the park as of December 2002 (Smith et al. 2003*b*). Elk constitute 92% of kills made by wolves in Yellowstone (Smith et al. 2003*b*).

**Data collection**

Elk group sizes were obtained by tracking 93 radiocollared cow elk using telemetry from a Supercub airplane. These elk were captured in March 2000, February 2001, and February 2002, from groups distributed throughout the Northern Range. They summered throughout most parts of the park and also north of the park on the Buffalo Plateau, suggesting that the groups associated with the radiocollared individuals were a representative sample of the cow groups of the entire population. The radiocollared cows and their associated groups were located and counted, on average, once per 12 days from 21 June 2000 to 1 November 2002. Group sizes were determined by counting individuals in groups of up to 30 elk or by approximating to the nearest 10 in larger groups. I assumed that observations of groups associated with the same radiocollared elk were independent at the 12-day interval of the counts, based on the observation that group composition varies freely as cow/calf units move among groups (Shoesmith 1979). Because all radiocollared animals were female, the findings of this study are applicable only to cow groups (including cow-calf, cow-bull, and cow-calf-bull groups).

**Seasons**

The study period was divided into calving, summer, rut, and winter seasons. Calving period was defined as mid-May to late June based on frequent observations of lone cows and cow/calf pairs. Summer was defined as early July, when most cows with calves rejoined larger elk groups, through late August. Rut,

during which groups were characterized by cows and calves with usually one herding bull, began in late August or early September, and lasted through the end of October. November through early May were winter months, when groups showed neither rutting nor calving behaviors, and were found on the Northern Range.

**Wolf density index**

An index representing wolf density was created from kernel estimators of wolf homeranges generated using the Animal Movement 2.0 extension in ArcView 3.2 (Hooge and Eichenlaub 1997). I used the *ad hoc* method (default setting in Animal Movement, based on Silverman 1996) for determining the smoothing parameters for the kernels. The output grid layers had a cell size of 100 meters and values ranging from low (6.9) to high (1580) wolf density index scores, representing up to 50 wolves/1000 $km^2$ (see main text and Figure 3 for more details). This index is an indirect measure of wolf predation risk, encapsulating an approximation of the probabilities of encounter, attack, and capture. Elk group locations were queried in ArcView for their respective seasonal wolf density index values.

**Habitat openness**

Habitat openness was defined as the percentage of open area within a 400-m radius of each elk group location. Four-hundred meters was the median distance at which elk responded when approached by humans, often fleeing

towards forest cover (Cassirer et al. 1992). I used the vegetation GIS layer (25-m cell size) developed for the Yellowstone grizzly bear Cumulative Effects Model (Dixon 1997). I consolidated vegetation types into open (i.e., non-forested) and forested (including burned forest) categories. For mosaic vegetation cells, I randomly chose one of the first 2 vegetation types.

**Typical group size**

The typical group size (TGS), which is the group size that the average individual experiences (Jarman 1974), was calculated for each season as:

$$TGS = \frac{\sum_{i=1}^{n} g_i^2}{\sum_{i=1}^{n} g_i},$$

where $g_i$ is the size of each of the $n$ groups observed. Equivalently, by dividing the numerator and denominator of equation above by $n$,

$$TGS = \frac{\text{mean}(g^2)}{\text{mean}(g)}.$$

The SE of a typical group size can be obtained through error propagation of the variances of $g^2$ and $g$ (Stuart and Ord 1994:351, eq. 10.17):

$$\text{SE}(TGS) = TGS * \sqrt{\frac{\sigma^2_{\text{mean}(g^2)}}{\text{mean}(g^2)} + \frac{\sigma^2_{\text{mean}(g)}}{\text{mean}(g)} - \frac{2}{\text{mean}(g^2) \times \text{mean}(g)} * \text{cov}(g^2, g)}.$$

**Group size models**

Generalized linear models were made for each season to predict *group size* as a function of *wolf density index* and *habitat openness*. Group size data were

natural log-transformed to fit a normal distribution, so all regressions used ln(*Group size*) as the response variable. I used the Akaike Information Criterion (AIC, Akaike 1974) to choose between 2 candidate models for each season, one with linear independent variables *wolf density index* and *habitat openness*, the other with log-transformed independent variables ln(*wolf density index*) and ln(*habitat openness* + 1). Back-transforming the models to obtain equations phrased in terms of *group size*, the candidate models took the form:

$$Group\ size = \exp[\beta_0 + \beta_1 * (wolf\ density\ index) + \beta_2 * (habitat\ openness)]$$

and

$$Group\ size = \exp(\beta_0) * (wolf\ density\ index)^{\beta_1} * (habitat\ openness + 1)^{\beta_2}$$

where $\beta_i$ are the regression coefficients.

**RESULTS**

3122 groups with radiocollared elk were located, of which 2809 groups were counted: 370 during calving season, 557 during summer, 461 during rut, and 1421 during winter. In 9%, 16%, 20%, and 4% of groups located during calving, summer, rut, and winter respectively, group size could not be determined because of low sightability due to tree cover or dense lodgepole pine regrowth in burned forests. In these cases, either no elk were seen at all, or some elk were spotted, but it was highly probable that the whole group was not visible.

Elk groups occurred mostly in forested habitats during calving, summer, and rut, but were found in mostly open habitats during winter (Figure 7). Elk

groups also occurred in lower wolf density areas during calving and summer, but experienced higher wolf densities in rut and especially winter (Figure 8).

Group sizes varied seasonally and showed very high variance within seasons (Figures 9 and 10, Table 8). The largest typical group size occurred in winter, with moderately sized groups in summer and smaller groups during calving and rut. Lone individuals and pairs were found during all seasons, most during calving season (Figure 9).

The models selected based on lower AIC score were:

Calving: $\textit{Group size} = \exp(1.63 + 0.000284 * \textit{Wolf density index} + 0.0115 * \textit{Habitat openness})$.

Summer: $\textit{Group size} = 3.78 * (\textit{Wolf density index})^{0.172} * (\textit{Habitat openness} + 1)^{0.131}$.

Rut: $\textit{Group size} = \exp(1.60 + 0.000433 * \textit{Wolf density index} + 0.0089 * \textit{Habitat openness})$.

Winter: $\textit{Group size} = \exp(2.08 + 0.000709 * \textit{Wolf density index} + 0.0120 * \textit{Habitat}$ openness).

In the models for calving, rut, and winter, group size is an exponential function of *wolf density index* and *habitat openness*, although in the calving and rut models, the functions are nearly linear within the range of *wolf density index* values because of small $\beta$ coefficients (Figure 11). In the summer model, group size is a logarithmic function of *wolf density index* and *habitat openness* (Figure 11).

## DISCUSSION

Typical group size was largest, as expected, during winter when both elk and wolf density were high, and when elk were on the mostly open landscape of the Northern Range. However, typical group size was smallest not during calving season, but rather during rut. During calving season, lone individuals and small

groups occurred in greater proportion than during the other seasons, but also larger groups existed that were similar in size to those found during summer. Many cows lose their calves quickly to predators (Singer et al. 1997), and likely rejoin larger groups shortly thereafter. Cows with calves also rejoin the herd 1-3 weeks after giving birth (Franklin and Lieb 1979), and benefit from the security of a larger group. During rut, however, herding of cows by bulls reduces the typical group size, which likely is influenced by the number of cows a bull can herd (Altmann 1956).

The variance of typical group size was extremely high for all seasons. Because of differences among individuals in competitive ability and baseline fitness (sensu Fretwell and Lucas 1970), not all elk may benefit from joining a group. Weak or otherwise conspicuous individuals are frequently targeted by pursuing predators (Krakauer 1995, Krause and Godin 1995, Mech et al. 2001), so odd individuals are expected to either leave a group or suffer a higher probability of depredation within the group. Prey oddity is one explanation offered for sexual segregation in species in which males and females are dimorphic (Geist 2002, Ruckstuhl and Neuhaus 2000), and also can account for exceptions such as observations of lone individuals and groups smaller than the theoretical optimal group size. The body condition of Northern Yellowstone cow elk varies widely (R. C. Cook, J. G. Cook, and L. D. Mech, unpublished paper). Consequently, high variation is expected in the anti-predator and foraging strategies of these elk, resulting in a parallel variability of group sizes.

Consistent with other studies of social ungulates (Knight 1970, Jarman 1974, Clutton-Brock et al. 1982, Heard 1992), elk in YNP formed larger groups in more open habitat. The higher sightability of elk in open versus forested habitats may exaggerate the relationship between group size and habitat openness; nevertheless, the positive correlation is realistic, assuming that more open habitat is less secure for elk (Geist 2002).

In all seasons, larger groups were associated with areas of higher wolf density. The differences in the shapes of the group size functions among seasons is likely attributable to seasonal differences in the vulnerability of elk to wolf predation. During calving and rut, elk tend to be in smaller groups because of reproductive activities, but their group size response to wolf density is more pronounced than during summer. Calving and rutting activities may make elk more vulnerable to predation than they otherwise would be. During calving, mothers must be especially vigilant to protect their young (Geist 2002). Once calves are old enough to join nursery groups, elk should benefit from joining large groups in the presence of high wolf density to increase their security from predation. During rut, bulls become preoccupied with herding cows and challenging other males (Geist 2002), and they also may distract cows from their ability to be vigilant. In higher wolf density areas, elk may need to form larger groups to compensate for their attention spent in rutting behaviors.

In the summertime, the response in elk group size to increasing wolf density is shallow compared to the other seasons. With calves more agile and alert than during their neonatal period and without rutting activities to engage

their time, cow and cow/calf groups may be relatively less vulnerable to wolf predation. Elk are distributed widely throughout the park at relatively low density in the summer and are able to select habitat that allows them to avoid wolves (see main text). They may not need to use grouping, in addition to habitat selection, to escape wolf predation.

In contrast, elk and wolf densities are at their highest in the winter, and elk are unable to use habitat selection to avoid wolves (see main text). Very large elk groups form likely because of a combination of high elk density, limited foraging areas in lower snow accumulation areas, and high wolf predation risk. Because elk body condition is low in winter (Cook 2002) and they must contend with high wolf density, elk are most vulnerable during this season. Elk group size in winter appears to respond strongly to wolf density, yielding the exponential shape of the group size function relative to *wolf density index*.

Alternatively, large elk groups may cause, rather than result from, high wolf density. Wolves are known to encounter and attack larger groups of elk compared to smaller groups (Huggard 1992, Hebblewhite and Pletscher 2002). Elk may gather according to patchy distribution of forage (e.g., Clarke et al. 1995), and wolves searching for elk are more likely to encounter larger elk groups. This scenario also would produce higher *wolf density index* values where larger elk groups are found, and may be the case especially during winter when elk distribution is concentrated on the lower snowpack areas of the Northern Range (see main text). Most likely, the patterns of elk group formation and wolf

distribution influence each other dynamically in a predator-prey "shell game" (Mitchell and Lima 2002).

As Bender and Haufler (1996) suggested, elk that have not experienced year-round predation pressure for several generations might not use grouping as an anti-predator strategy. Upon the restoration of a major predator, however, behavioral adaptations in prey should return quickly (Berger 2001). Elk in YNP have an array of anti-predator defenses used to avoid wolf predation, including vigilance (Laundré et al. 2001, Wolff and Van Horn 2003), habitat selection (see main text), and grouping.

Table 1. Percent availability of vegetation types[a] on summer and winter ranges.

| Vegetation type | Summer | Winter |
|---|---|---|
| Grass | 12 | 15 |
| Shrub | 11 | 40 |
| Other Nonforest | 5 | 4 |
| Aspen | 0 | 1 |
| Burned Conifer[b] | 2 → 27 | 0 → 6 |
| Unburned Conifer[b] | 70 → 45 | 42 → 34 |

[a] Minimum mapping resolution was approximately 2 ha (Dixon 1997), although the cell size of the GIS grid layer was 25 m.

[b] Before → after 1988 fires.

Table 2. Continuous variables used to predict habitat selection. Median, minimum, and maximum values are based on random (available) points.

| | | Summer | | | Winter | | |
|---|---|---|---|---|---|---|---|
| Variable | GIS grid cell size (m) | Median | Min | Max | Median | Min | Max |
| Openness (%) | 25 | 9 | 0 | 100 | 63 | 0 | 100 |
| Elevation (m) | 30 | 2477 | 1639 | 3334 | 2130 | 1544 | 3034 |
| Slope (degrees) | 30 | 10 | 0 | 72 | 12 | 0 | 66 |
| Wolf Density Index | 100 | 142.2 | 6.9 | 1564.0 | 466.4 | 8.8 | 1564.2 |
| SWE (cm) | 100 | | | | 4.4 | 0.0 | 71.7 |

Table 3. Mean annual Keetch-Byram Drought Index (KBDI) based on Tower Falls, Canyon, Yellowstone Lake, Parker Peak, and Old Faithful weather stations. Paired *t*-tests compare each year's mean KBDI against the 1961-1990 long-term mean KBDI, pairing by weather station.

| Year | Mean KBDI | SE | *t* | *P* |
|---|---|---|---|---|
| 1985 | 49 | 13 | -0.91 | 0.42 |
| 1986 | 34 | 7 | -2.55 | 0.06 |
| 1987 | 36 | 7 | -2.42 | 0.07 |
| 1988 | 78 | 17 | 3.39 | 0.03 |
| 1989 | 64 | 14 | 1.49 | 0.21 |
| 2000 | 47 | 5 | -0.93 | 0.40 |
| 2001 | 33 | 5 | -3.02 | 0.04 |
| Long-term | 55 | 11 | | |

Table 4. *A priori* candidate models for summer habitat selection by elk.

| Model # | Model structure[a] | -2LL | K | $\Delta_i$ | $w_i$ |
|---|---|---|---|---|---|
| Prewolf: | | | | | |
| NW-1 | VEG | 8532 | 5 | 261.7 | 0.0 |
| NW-2 | ELEV + VEG | 8242 | 7 | 155.8 | 0.0 |
| NW-3 | SECURITY + VEG | 8381 | 9 | 119.2 | 0.0 |
| NW-4 | ELEV + SECURITY + VEG | 8258 | 11 | 0.0 | 1.0 |
| Postwolf-NW: | | | | | |
| NW-1 | VEG | 11158 | 5 | 188.3 | 0.0 |
| NW-2 | ELEV + VEG | 11026 | 7 | 59.5 | 0.0 |
| NW-3 | SECURITY + VEG | 11103 | 9 | 141.2 | 0.0 |
| NW-4 | ELEV + SECURITY + VEG | 10958 | 11 | 0.0 | 1.0 |
| Postwolf-W: | | | | | |
| W-1 | WOLF + VEG | 11141 | 7 | 179.2 | 0.0 |
| W-2 | WOLF + ELEV + VEG | 11020 | 9 | 62.0 | 0.0 |
| W-3 | WOLF + SECURITY + VEG | 11085 | 11 | 130.7 | 0.0 |
| W-4 | WOLF + ELEV + SECURITY + VEG | 10953 | 13 | 2.9 | 0.2 |
| W-2i | WOLF + ELEV + WOLF*ELEV + VEG | 11020 | 10 | 63.6 | 0.0 |
| W-3i | WOLF + SECURITY + WOLF*SECURITY + VEG | 11081 | 13 | 130.5 | 0.0 |
| W-4i | WOLF + ELEV + WOLF*ELEV + SECURITY + WOLF*SECURITY + VEG | 10944 | 16 | 0.0 | 0.8 |

[a] VEG = Vegetation categories, ELEV = Elevation + Elevation$^2$, SECURITY = Openness + Openness$^2$ + Slope + Slope$^2$, WOLF = Wolf Density Index + Wolf Density Index$^2$.

Table 5. *A priori* candidate models for winter habitat selection by elk.

| Model # | Model structure[a] | -2LL | K | $\Delta_i$ | $w_i$ |
|---|---|---|---|---|---|
| Prewolf: | | | | | |
| NW-1 | SNOW + VEG | 6127 | 7 | 142.6 | 0.0 |
| NW-2 | SECURITY + SNOW + VEG | 5977 | 11 | 0.0 | 1.0 |
| Postwolf-NW: | | | | | |
| NW-1 | SNOW + VEG | 8731 | 7 | 240.0 | 0.0 |
| NW-2 | SECURITY + SNOW + VEG | 8483 | 11 | 0.0 | 1.0 |
| Postwolf-W: | | | | | |
| W-1 | WOLF + SNOW + VEG | 8655 | 9 | 269.1 | 0.0 |
| W-2 | WOLF + SECURITY + SNOW + VEG | 8428 | 13 | 50.1 | 0.0 |
| W-1i | WOLF + WOLF*SNOW + SNOW + VEG | 8641 | 10 | 257.3 | 0.0 |
| W-2i | WOLF + SECURITY + WOLF*SECURITY + SNOW + WOLF*SNOW + VEG | 8372 | 16 | 0.0 | 1.0 |

[a] SNOW = Snow Water Equivalents, VEG = Vegetation categories, SECURITY = Openness + Openness$^2$ + Slope + Slope$^2$, WOLF = Wolf Density Index + Wolf Density Index$^2$.

Table 6. Selected summer habitat selection models. Grassland is the reference category for the vegetation variable.

| | Prewolf habitat selection[a] | | | Postwolf-NW habitat selection[b] | | | Postwolf-W habitat selection[c] | | |
|---|---|---|---|---|---|---|---|---|---|
| Variable | β | SE | p | β | SE | p | β | SE | p |
| Shrubland | -0.09 | 0.10 | 0.387 | -0.04 | 0.13 | 0.751 | -0.02 | 0.14 | 0.864 |
| Other nonforest | -1.30 | 0.33 | <0.001 | -0.72 | 0.18 | <0.001 | -0.71 | 0.18 | <0.001 |
| Burned forest[d] | -0.86 | 0.16 | <0.001 | 0.25 | 0.11 | 0.029 | 0.26 | 0.11 | 0.023 |
| Unburned forest[e] | -0.24 | 0.11 | 0.026 | -0.20 | 0.11 | 0.064 | -0.19 | 0.11 | 0.072 |
| Openness | 0.013 | 0.001 | <0.001 | -0.003 | 0.002 | 0.055 | -0.003 | 0.002 | 0.080 |
| Elevation | 0.026 | 0.003 | <0.001 | 0.006 | 0.002 | 0.010 | 0.006 | 0.002 | 0.012 |
| Elevation$^2$ | -5.27E-06 | 5.33E-07 | <0.001 | -8.43E-07 | 4.51E-07 | 0.062 | -8.10E-07 | 4.49E-07 | 0.071 |
| Slope | 0.010 | 0.012 | 0.427 | 0.021 | 0.010 | 0.042 | 0.013 | 0.011 | 0.253 |
| Slope$^2$ | -0.0014 | 0.0004 | 0.001 | -0.0014 | 0.0003 | <0.001 | -0.0014 | 0.0003 | <0.001 |
| Slope * Wolf Density | | | | | | | 3.19E-05 | 1.41E-05 | 0.024 |
| Wolf Density | | | | | | | -0.00048 | 0.00021 | 0.023 |
| -2LL | 8276 | | | 10959 | | | 10952 | | |
| K | 10 | | | 10 | | | 12 | | |
| $\Delta_i$[f] | -15.7 | | | -1.1 | | | -0.2 | | |
| k-fold rho (*P*) | 0.93 (<0.002) | | | 0.81 (<0.01) | | | 0.85 (<0.01) | | |

[a] *Post hoc* model modified from *a priori* prewolf summer model # NW-4.
[b] *Post hoc* model modified from *a priori* postwolf summer model # NW-4.
[c] *Post hoc* model modified from *a priori* postwolf summer model # W-4i.
[d] Burned aspen + burned conifer.
[e] Unburned aspen + unburned conifer.
[f] Relative to $AIC_c$ of the best *a priori* candidate model.

Table 7. Selected winter habitat selection models. Grassland is the reference category for the vegetation variable.

| | Prewolf habitat selection[a] | | | Postwolf-NW habitat selection[b] | | | Postwolf-W habitat selection[c] | | |
|---|---|---|---|---|---|---|---|---|---|
| Variable | β | SE | p | β | SE | p | β | SE | p |
| Aspen[d] | 0.13 | 0.27 | 0.638 | 0.70 | 0.17 | <0.001 | 0.69 | 0.17 | <0.001 |
| Shrubland | 0.16 | 0.11 | 0.132 | -0.12 | 0.08 | 0.127 | -0.17 | 0.08 | 0.036 |
| Other nonforest | -0.88 | 0.25 | 0.001 | -1.61 | 0.25 | <0.001 | -1.38 | 0.25 | <0.001 |
| Burned conifer | -0.64 | 0.30 | 0.033 | -0.10 | 0.16 | 0.515 | -0.14 | 0.16 | 0.383 |
| Unburned conifer | 0.14 | 0.13 | 0.272 | 0.03 | 0.11 | 0.787 | -0.01 | 0.11 | 0.950 |
| Openness | 0.044 | 0.005 | <0.001 | 0.032 | 0.004 | <0.001 | 0.029 | 0.004 | <0.001 |
| Openness$^2$ | -3.83E-04 | 3.98E-05 | <0.001 | -2.22E-04 | 3.37E-05 | <0.001 | -2.12E-04 | 3.37E-05 | <0.001 |
| Slope | 0.028 | 0.013 | 0.035 | 0.059 | 0.012 | <0.001 | 0.100 | 0.015 | <0.001 |
| Slope$^2$ | -0.0016 | 0.0004 | <0.001 | -0.0031 | 0.0004 | <0.001 | -0.0033 | 0.0004 | <0.001 |
| Slope * Wolf Density | | | | | | | -6.12E-05 | 1.08E-05 | <0.001 |
| Snow | -0.13 | 0.01 | <0.001 | -0.13 | 0.01 | <0.001 | -0.07 | 0.01 | <0.001 |
| Snow * Wolf Density | | | | | | | -1.05E-04 | 2.35E-05 | <0.001 |
| Wolf Density | | | | | | | 0.0033 | 0.0004 | <0.001 |
| Wolf Density$^2$ | | | | | | | -1.04E-06 | 2.39E-07 | <0.001 |
| -2LL | 5977 | | | 8483 | | | 8373 | | |
| K | 11 | | | 11 | | | 15 | | |
| $\Delta_i$[e] | 0.0 | | | 101.4 | | | -0.4 | | |
| k-fold rho (*P*) | 0.92 (<0.002) | | | 0.96 (<0.002) | | | 0.93 (<0.002) | | |

[a] *A priori* prewolf winter model # NW-2.
[b] *A priori* postwolf winter model # NW-2.
[c] *Post hoc* model modified from *a priori* postwolf winter model # W-2i.
[d] Burned + unburned aspen.
[e] Relative to the $AIC_c$ of the best *a priori* candidate model.

Table 8. Typical group sizes and maximum observed group sizes of elk in Yellowstone National Park, Wyoming, 21 June 2000 to 1 November 2003.

| Season | n | Typical group size (SE) | Maximum |
|---|---|---|---|
| Calving | 370 | 57 (211) | 200 |
| Summer | 557 | 85 (386) | 350 |
| Rut | 460 | 39 (243) | 200 |
| Winter | 1422 | 199 (702) | 700 |

Figure 1. Summer herd segments areas defined by 95% kernel home ranges.

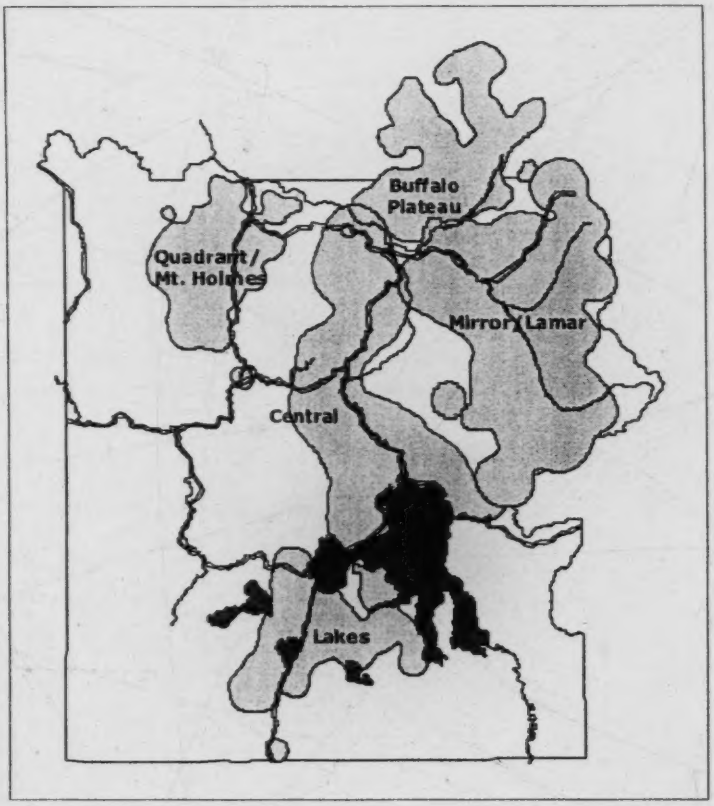


Figure 2. Winter sections of the Northern Range defined by 95% kernel home ranges. The Northern Range boundary is outlined (and shown in the inset in gray). Overlapping areas among the winter kernel polygons were removed so that the polygons conformed to predefined geographic boundaries between sections (Gardner River and Crevice Mountain between Lower and Middle NR, Yellowstone River between North and South Middle NR, Lamar Canyon and Yellowstone River between Middle and Upper NR).

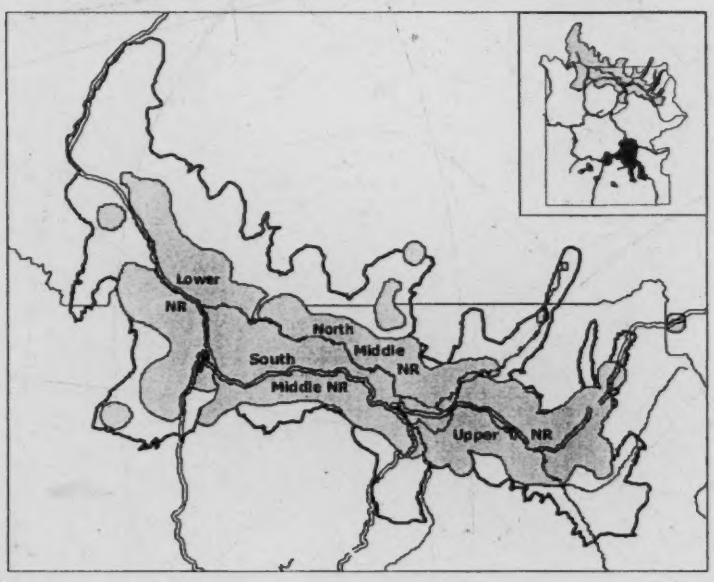


Figure 3. Examples of wolf density index maps for (a) early summer 2001, (b) mid-summer 2001, (c) late summer 2001, and (d) winter 2001/02. Darker areas indicate higher wolf density, up to 50 wolves per 1000 $km^2$ (Smith et al. 2003).

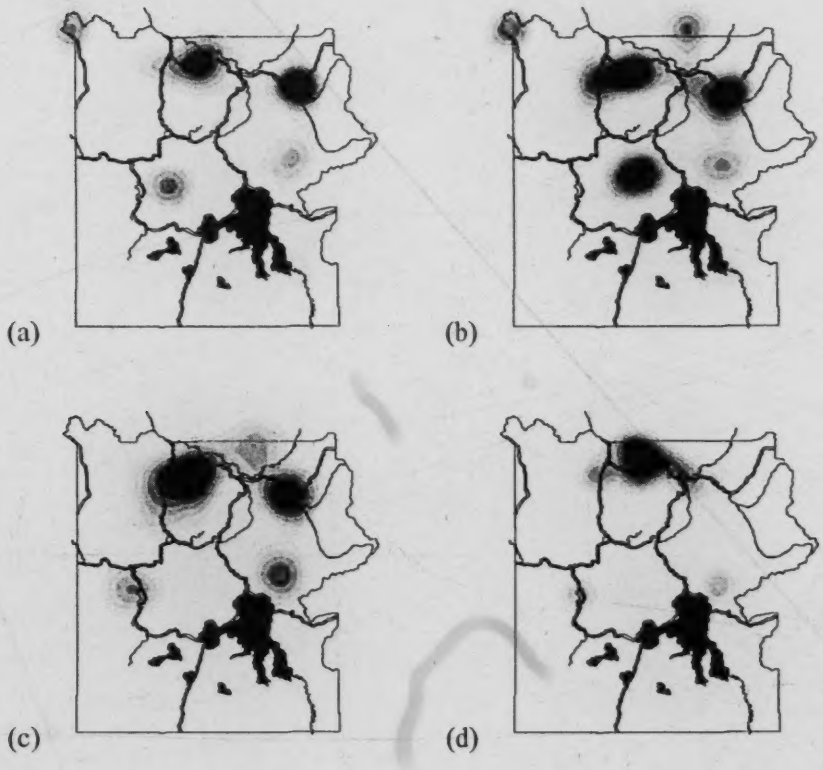


Figure 4. Postwolf selection of slope in summer. Solid lines are partial RSF values with respect to slope predicted by the summer postwolf-W model at wolf density index levels ranging from 0 to 1600 (light to dark lines). The dashed line is the partial RSF with respect to slope predicted by the summer postwolf-NW model.

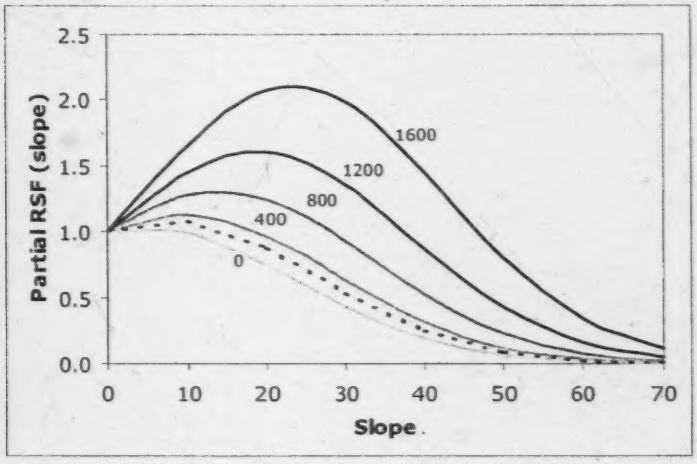


Figure 5. Postwolf selection of slope in winter. Solid lines are partial RSF values with respect to slope predicted by the winter postwolf-W model at wolf density index levels ranging from 0 to 1600 (light to dark lines). The dashed line is the partial RSF with respect to slope predicted by the winter postwolf-NW model.

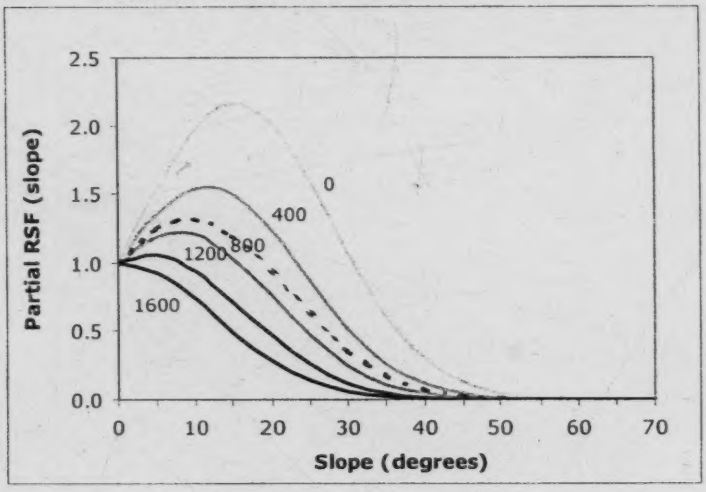



Figure 6. Postwolf selection of snow water equivalent (SWE) in winter. Solid lines are partial RSF values with respect to SWE predicted by the winter postwolf-W model at wolf density index levels ranging from 0 to 1600 (light to dark lines). The dashed line is the partial RSF with respect to SWE predicted by the winter postwolf-NW model.

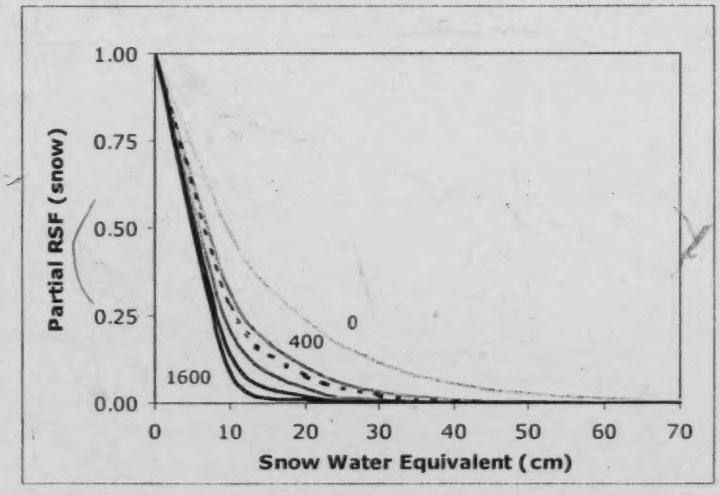


Figure 7. Frequency distribution of Northern Yellowstone elk groups relative to habitat openness.

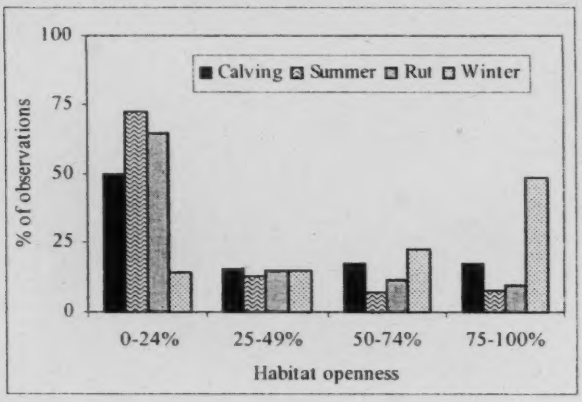



Figure 8. Frequency distribution of Northern Yellowstone elk groups relative to wolf density index. The categories of wolf density index are low (6.9-399), medium (400-799), high (800-1199), and very high (1200-1580), corresponding to a maximum estimated wolf density of 50 wolves/1000 $km^2$.

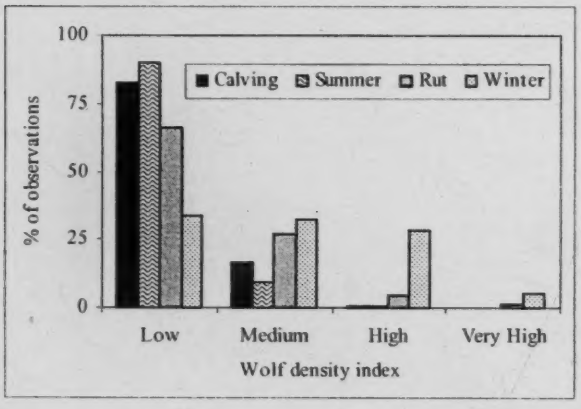


Figure 9. Frequency distribution of group size classes of Northern Yellowstone elk by season.

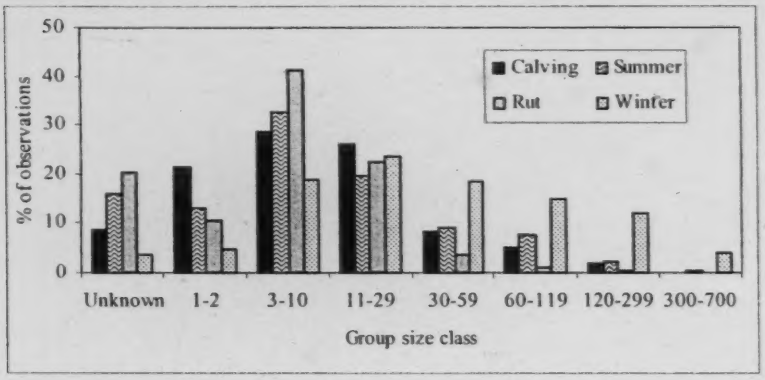



Figure 10. Typical group sizes of Northern Yellowstone elk by month.

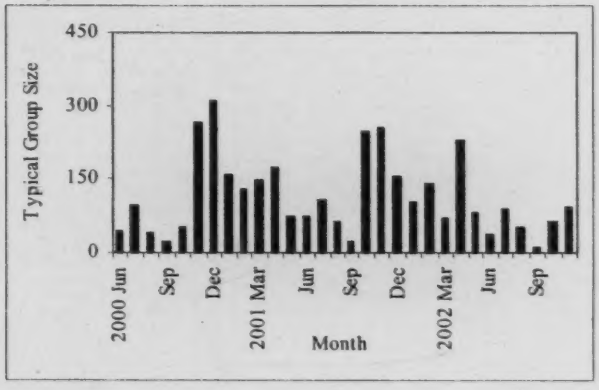
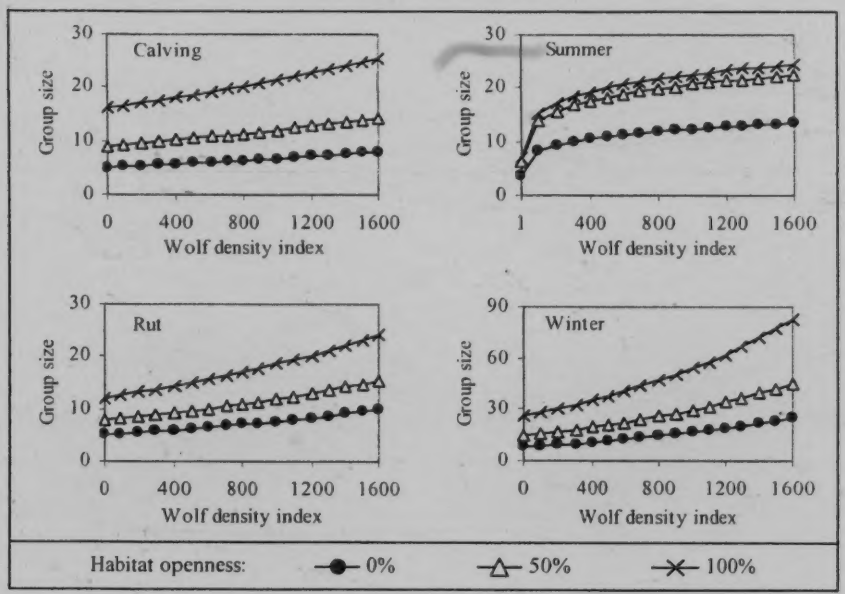


Figure 11. Elk group size predictions as functions of *wolf density index* and *habitat openness* in Yellowstone National Park, Wyoming.



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